

REVIEW

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Physiological effects of resistant starch and its applications in food: a review

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Abstract

Starch, as the main source of carbohydrates in the diet, provides energy for various activities of the body. Different types and structures of starch lead to variations in digestion and absorption, thereby affecting blood glucose levels and lipid metabolism in the body. Resistant starch (RS) has gained much attention because of its unique properties; it is not digested in the small intestine but ferments in the large intestine and produces short-chain fatty acids. RS has been found to play a crucial role in glucose homeostasis, fat metabolism, cholesterol levels and mineral absorption. Furthermore, RS has a high thermal stability, white color and low water holding capacity, making it useful in a wide range of food industry applications. This review aims to provide an update on the physiological effects of RS under physiological and pathological conditions, to provide information on the applications of RS in the food industry, and to assess whether dietary strategies to improve RS could have potential prevention and therapeutic effects for metabolic disorders associated with diabetes, obesity, and hyperlipidemia.

Keywords Resistant starch, Short-chain fatty acid, Glucose homeostasis, Gut microbiota, Food

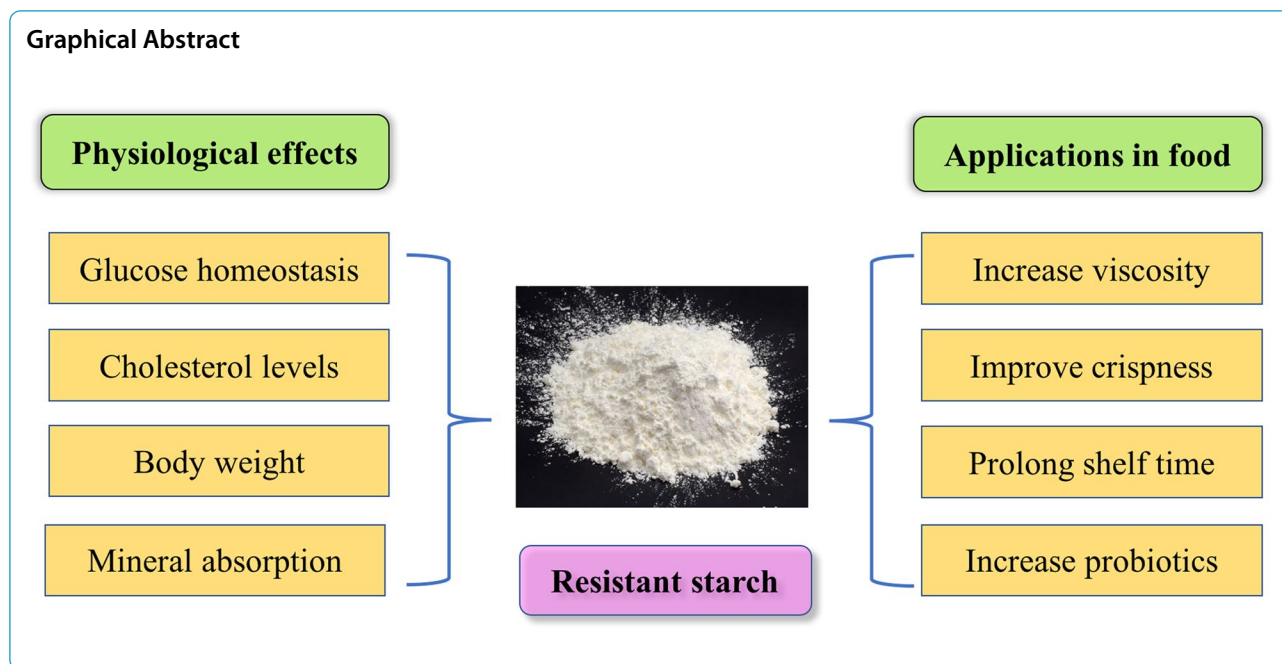
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Introduction

Resistant starch (RS) refers to starch and its degradation products that are not absorbed by the small intestine of healthy humans. Since its discovery in 1985, studies on the regulation of RS on metabolic homeostasis and the gut microbiome have dramatically increased. Since then, different animal models have been used to demonstrate its important roles in metabolic disorders. It has been reported that RS functions as a key regulator of blood glucose, cholesterol metabolism, and the intestinal flora and exerts potential positive impacts on diseases associated with metabolic disorders, including obesity, diabetes and hyperlipidemia (Englyst et al. 1992; Birt et al. 2013).

With the development of the economy and changes in lifestyle, the incidence of metabolic disorders such as diabetes and obesity has markedly increased, which accelerates the occurrence of cardiovascular, cerebrovascular and renal diseases and seriously affects quality of life. The common feature of obesity and diabetes is disrupted energy metabolism; therefore, energy intake regulation through an appropriate diet is the key to preventing these diseases. RS has been emerged as a crucial player in the regulation of blood glucose, lipids, and gut microbiota due to its unique way of digestion and absorption (Hemmingsen et al. 2017; Koh & Rowling 2017).

Although studies on RS have been increasing during the last few years, a comprehensive update on the issue about the physiological effects of RS and its application in food are still lacking. In this review, we aimed (i) to summarize the important roles of RS in maintaining glucose homeostasis, fat metabolism, cholesterol levels, mineral

absorption, and regulation in metabolic disorders, (ii) to discuss the conflicting results about the effects of RS on metabolic disorders and (iii) to analyze the possible reasons for the conflicting results. Finally we discussed the potential mechanisms that involved in the positive impacts of RS on gut health and forecasted the trends of further research to gain a better understanding of the physiological effects of RS and its applications in food.

Types of RS

RS is divided into five classes based on its source, structure, and digestive properties. RS1 is classified due to the physically protected structure which blocks the accessibility of digestive enzymes. RS2 is classified based on the native starch granules with compact B-type crystallinity. RS3 is classified as the linear structure of amylose molecules transformed into double helices during the cooling of starchy food. RS4 is classified when the starch is chemically modified through cross-linking and or esterification. RS5 is classified as the long chain parts of amylose and amylopectin of starch interact with lipids and form the amylose-lipid complex (Englyst et al. 1992; Raigond et al. 2015).

RS1

RS1 is a physically encapsulated starch, wherein the starch granules are wrapped by plant cell walls or proteins to form a physical barrier, which prevents it from contacting digestive enzymes so it cannot be digested and absorbed in the small intestines. This type of starch primarily exists in foods such as grains and beans with

insufficient milling and coarse particles. When starch is cooked in the form of whole grains, the cell walls of legume seeds and the proteins of the grain hinder the penetration of water into the starch, and the starch cannot obtain sufficient water for swelling and gelatinization, which makes it difficult to combine with amylase for hydrolysis (Jenkins et al. 1988). Changes in the processing method can affect its resistance and make it easier to digest (Bao et al. 2018; Sun et al. 2022).

RS2

RS2 is a RS granule that has a B-type or C-type crystal-embedded compact molecular structure, making it inaccessible to amylase (Baker et al. 2001). This type of RS is mainly found in bananas, raw rice, raw flour and potatoes, as well as high amylose corn starch. Processing methods such as cooking and pulverization can increase the action of digestive enzymes and reduce the content of RS. Most starch will lose the B-type or C-type crystalline structure through gelatinization after cooking and become fast-digesting starch, such as occurs with baked potatoes (Noor et al. 2021).

RS3

RS3 is an aged starch, also known as retrograded starch, which is the most common type of RS. It is formed by the aging and regeneration of amylose during food processing. Under freezing conditions, starch undergoes retrogradation, and the long chains of amylose molecules and amylopectin recombine to form double helical polymers connected by hydrogen bonds, forming short linear crystals with a strong molecular structure that make it difficult to degrade by amylase in the gastrointestinal tract (Jane & Robyt 1984). Aged starch has good thermal stability, low water holding capacity and better taste than traditional dietary fiber. As an auxiliary raw material, it has little effect on the color and flavor of food, as well as the original nutrient elements during cooking and heating processes, which makes it a new type of food ingredient with wide application prospects (Witt et al. 2010; Zeng et al. 2015; Li et al. 2021).

RS4

RS4 is a chemically modified starch that is formed by introducing new chemical groups to natural starch. Among these modifications are esterification, phosphorylation, ethyl esterification, or γ -ray irradiation, which lead to changes in the molecular structure and physical and chemical properties of starch, preventing the adsorption of amylase or the formation of cross-links. Common modified starches are heat-denatured starch, cross-linked starch, acetyl starch, and phosphorylated starch (Hsieh et al. 2020; Yaver & Bilgicli 2021). Modified starches have

textural properties suitable for a variety of food processing; for example, acetylated starch is gelatinous at low temperature, which makes it ideal for adding to gravies, pie fillings and salad dressings; phosphated starch has good freeze–thaw stability and is often used in frozen foods; and cross-linked starch is often used as a thickener in canned foods (Falsafi et al. 2019).

RS5

RS5 is an amylose-lipid complex formed by combining amylose with fatty acids or fatty alcohols. RS5 usually has a V-shaped crystal structure, and its unique crystal structure reduces the contact area between the starch granules and digestive enzymes, thus causing it to be indigestible. Such complexes are commonly found in native starches such as grains, soybeans, and corn, and their content can be increased by high temperature, they can be prepared by the addition of lipids under laboratory conditions (Putseys et al. 2010; Okumus et al. 2018). RS5 has a high gelatinization temperature and strong thermal stability and is prone to retrogradation (Gelders et al. 2006).

The physiological effects of RS

Impacts of RS on glucose levels and diabetes

Diabetes is a metabolic disease in which blood glucose levels are abnormally elevated. The number of diabetic patients has increased significantly in recent years, and its prevention and treatment have become major public health issues worldwide. Approximately 90–95% of diabetes patients have type II diabetes, and dietary intervention is an important part of the treatment. The diet of diabetic patients, especially the selection and control of staple foods, including the primary source of carbohydrates, is the basis of diabetes treatment (Chan et al. 2009; Hemmingsen et al. 2017; Zheng et al. 2018). The indigestion of RS in the small intestine decreases the glycemic index after ingestion, and the fluctuation of postprandial blood glucose is small, which effectively improves the glucose tolerance level of diabetic patients (Dainty et al. 2016; Maziarz et al. 2017; Arias-Cordova et al. 2021). It has been shown that RS2 is effective in regulating fasting insulin concentrations and insulin resistance in diabetes patients (Dainty et al. 2016). RS3-containing feed markedly reduced the release of glucose-dependent insulinotropic polypeptides, serum glucose and insulin levels in type II diabetic rats, thereby ameliorating the metabolism of glucose (Sun et al. 2018; Qadir et al. 2020). Postprandial plasma glucose concentrations and insulin responses were significantly reduced when overweight adults were given bread containing 60% RS (Yamada et al. 2005; Takahashi et al. 2022). However, a 12-week double blind clinical study found that RS2 supplementation had no significant difference in glycemic

control compared with rapidly digestible starch in overweight adults with prediabetes. We speculate that this paradoxical result may be due to the complexity of the causes of diabetes itself and the disorganized gut flora of obese populations that cannot interact well with RS. Therefore, more precise and personalized RS intake strategies are needed to improve diabetes in different populations.

Impacts of RS on gastrointestinal health

RS has been shown to promote gastrointestinal motility, to shorten the transit time of intestinal contents, and to increase defecation volume; hence, it helps prevent the occurrence of constipation (Qian et al. 2013; Wang et al. 2014). It was demonstrated that RS increased the volume of excrement and reduced intestinal pH in rats (Clarke et al. 2008; Patten et al. 2015). The fermentation products of RS mainly include short-chain fatty acids, such as formic acid, acetic acid, and butyric acid. These substances play important roles in nourishing the colonic mucosa because they can provide energy for the colonic mucosa. RS5 effectively inhibited the precancerous lesions of the rat colon induced by azomethane (Zhao et al. 2011; Cray et al. 2017). RS5 increased the volume and hydrophobicity of rat feces, which was beneficial for the excretion of toxic chemicals (Kleessen et al. 1997). It was reported that dietary RS increased the barrier function of ileum by reducing permeability and up-regulating the expression of Mucin-2 and tight junction proteins in duck. The results of metabolomics showed that the different metabolites in RS diet treatment group were mainly associated with amino acid and lipid metabolism, vitamin metabolism pathway, intestinal inflammation, contributing to a better understanding of that how RS improves intestinal health (Qin et al. 2023). This study implied that microbiomes play a major role in determining the outcomes of RS supplementation and further study needs to explore more deeply into the mechanisms of RS digestion. A randomized controlled trial found that the RS diet does affect the intestinal flora through phylogenetic chip and quantitative PCR analysis, but the diet only partially explained the composition of the microbiota, far less than the differences among individuals (Salonen et al. 2014). The results of this study suggest that there are considerable differences in the response of individual microbial flora to the diet and this is an important factor that cannot be ignored when evaluating the effects of RS on intestinal integrity.

Impacts of RS on body weight and obesity

Obesity is a worldwide health issue characterized by the excessive accumulation of fat from food intake or abnormal metabolism (Haslam & James 2005; Collaboration

2017). Reducing energy intake is an effective way to control weight, and growing evidence suggests that RS contributes to weight management (Hu et al. 2018; Liu et al. 2020). RS is difficult to degrade into glucose, which is directly utilized by the human body, so the energy produced by RS is very low, at only approximately 10% of digestible starch (Higgins 2014). RS can reduce food intake by increasing the secretion of satiety-related hormones such as glucagon-like peptide-1 (GLP-1) and peptide tyrosine tyrosine (PYY) (Keenan et al. 2006; Zhou et al. 2008). It was found that muffins with a high RS content stimulated satiety, prolonged the digestion time and resulted in weight loss (Maziarz et al. 2017). Replacing carbohydrates with RS led to a significant increase in postprandial fat oxidation (Higgins et al. 2004), suggesting that RS could reduce fat accumulation. RS-containing diets significantly reduced the energy intake and body weight of rats (Belobrajdic et al. 2012). RS also significantly reduced body weight in obese rats (Higgins et al. 2011). Thus, these studies indicate that RS exerts positive effects on the control of body weight by reducing energy and fat accumulation and increasing satiety.

Impacts of RS on cholesterol homeostasis

Since cholesterol is essential for cell membrane formation and the synthesis of steroid hormones and vitamin D, it is important to maintain homeostasis in the body (Luo et al. 2020). However, excessive intake of high caloric foods leads to increased levels of cholesterol and triglycerides in plasma and causes hyperlipidemia, which is a crucial risk factor for atherosclerotic cardiovascular disease (Schade et al. 2020). Among the large amounts of short-chain fatty acids produced by RS fermentation, propionic acid plays a major role in lowering cholesterol and affecting lipid absorption and fatty acid synthesis (Cheng & Lai 2000). Several studies have shown that the intake of RS is positively correlated with the level of propionic acid in serum. Propionic acid reduces low-density lipoprotein and cholesterol levels in the serum and liver in rats (Fukushima et al. 2001; Han et al. 2003; Yuan et al. 2018). RS increases short-chain fatty acids and reduced plasma total cholesterol and triglyceride levels in rodents (Kleessen et al. 1997; Le Thanh-Blicharz et al. 2014), which indicates that RS has a positive effect on lowering cholesterol levels. Butyric acid produced by RS fermentation increases the excretion of bile acid compounds, enhances the activity of bile acid hydrolase, and reduces lipid absorption, which in turn increases free fatty acids in feces (van Munster et al. 1994). When patients with metabolic syndrome were given an RS-containing diet, plasma triglyceride levels were significantly reduced (Johnston et al. 2010). However, a recent study reported that RS intake has little effect on human total cholesterol

levels (Liu et al. 2021). Therefore, more research is needed to understand the effects of RS on lipid metabolism in humans. It was found that RS3 intervention ameliorated dyslipidemia and cecal environment of mice that fed a high-fat diet. RS3-*Novelose 330* decreased food intake and body weight, low-density lipoprotein cholesterol and serum total cholesterol, promoted the growth of the main butyrate producing bacteria in *Lachnospiraceae*, *Roseburia* and *Bifidobacterium*, which indicated that the positive effects of RS3 in regulating serum lipids is associated with the intestinal microflora and production of short chain fatty acids (Chen et al. 2023). Lotus seed RS administration to hyperlipidemia rats had been shown to improve blood lipid levels by modulating the structure small intestinal flora and accelerating the conversion of cholesterol into bile acids, which provides important insights on how RS regulates blood lipid by regulating intestinal microbiome.

Impacts of RS on minerals absorption and utilization

Mounting evidence shows that RS promotes the absorption and utilization of minerals, vitamins and other nutrients (Schulz et al. 1993; Lattimer & Haub 2010; Zeng et al. 2017). On the one hand, the short-chain fatty acids produced by RS fermentation reduce the pH in the colon, accelerating the transformation of mineral elements into soluble ions that are easily absorbed (Lesmes et al. 2008; Metzler-Zebeli et al. 2019). Rat diets with an increasing proportion of RS enhanced the solubility of iron in the cecum contents (Orzel et al. 2007), indicating that RS promoted the absorption of iron and might have a positive effect on alleviating iron deficiency. On the other hand, short-chain fatty acids accelerate the proliferation rate of intestinal epithelial cells and enlarge the intestinal wall, thereby promoting the absorption and utilization of minerals (Nofrarias et al. 2007; Fu et al. 2019). It was found that RS significantly promoted the absorption of calcium and iron ions in the intestine (Morais et al. 1996). Feed rich in RS significantly improved the absorption of calcium and iron when compared to fully digestible starch. In addition, the phytic acid contained in dietary fiber has a highly antagonistic effect on mineral absorption, whereas RS does not contain phytic acid and allows for more efficient digestion and absorption of minerals (Yonekura & Suzuki 2005).

Applications of RS in food

Due to its unique characteristics, including natural origin, low water holding capacity, high gelatinization temperature, and good extrusion performance, RS has a wide range of applications in foods. RS3 prevents fat absorption and loss of moisture content during frying. RS4 has been reported to hinder the formation of gel

networks and to reduce the hardness of food that can be used in baked food. Foods rich in dietary fiber generally have poor palatability, while RS has little effect on the taste of the food itself. In addition, RS can also be used as a thickener for soup to effectively improve sensory quality. Furthermore, the low water holding capacity of RS contributes to prolonging the shelf life of foods (Wongsagonsup et al. 2014; Patterson et al. 2020; Robertson et al. 2021).

Adding RS to partially replace the starch improves the water retention capacity of sausage. This is because the strong permeability of RS causes water to penetrate into the RS granules and form hydrogen bond hydrates with the free hydroxyl groups. RS forms a gel with myosin in meat, which helps to retain the moisture and flavor of meat products (Raigond et al. 2015; Sarteshnizi et al. 2017). RS has been proven to be a suitable substrate for the production of probiotics. Yogurt containing RS has a higher number and survival rate of lactobacilli, indicating that RS enhances the health benefits of yogurt (Aryana et al. 2015). In addition, the addition of RS increases the viscosity and sensory properties of yogurt (He et al. 2019). Replacing refined flour with RS in bread effectively reduces postprandial glucose and insulin responses in humans (Mohebbi et al. 2018; Lee et al. 2020). In addition, RS application contributes to increasing the water absorption of doughs and reducing the viscoelasticity of noodles, which can increase satiety and reduce digestible carbohydrate intake (Lee et al. 2020; Yaver & Bilgicli 2021; Li et al. 2022). RS has a high heat resistance, so RS can be used in fried food to improve the crispness of food and reduce the adverse effects of the Maillard reaction on food nutritional quality (Wang et al. 2016).

Conclusions

The study provides an overview of the physiological effects of RS and its applications in the food industry, revealing the role of RS in modulating glucose homeostasis, energy intake, cholesterol metabolism and the intestinal flora and showing the potential positive impacts on metabolic disorders and gut health. Despite the recent progress discussed in this review, some questions remain to be resolved. First, the reasons for these physiological effects of RS remain unclear. Therefore, it is necessary to elucidate how RS is digested and absorbed under physiological conditions, including which enzymes digest it at which sites in the digestive tract and what metabolites are produced. Based on this, further research needs to investigate the underlying mechanism of RS actions at the gene, protein and metabolic levels by omics technique, which would provide insights into how RS functions in gut health and metabolic disorders. Second, explore the fine structure

of different types of RS the relationship between different types of RS structures and physiological effects. For the prevention and treatment of metabolic disorders, the long-term clinical data are needed, and cautions need to be paid that not everyone receives the same benefits and not all types of RS exert the same effects, so the more precise and personalized solutions are needed. In addition, efficient methods for RS preparation need to be established. Understanding these questions will undoubtedly provide substantial advances in our understanding of RS.

Authors' contributions

JH and JRS conceived the content of the review, JH wrote the manuscript. JRW, XL, JRS, JHX contributed to manuscript review and revision. All authors read and approved the final version of the manuscript.

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Availability of data and materials

All data supporting this review are included in the reference part.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

Dr. Jianrong Shi is a member of Editorial Board of *Food Production, Processing and Nutrition* and he was not involved in the journal's review of, or decisions related to this manuscript.

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